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SEX-LIMITED CHARACTERS AND ALLOSOME-LINKED HEREDITY*.

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In developing a general theory of sex, it is necessary to consider all the fundamental phenomena of sexuality which occur in all the diverse types of plants and animals with their diverse types of life cycles, times of chromosome reduction, and diploid and haploid generations, otherwise a very incomplete or improper view of the subject will surely be obtained. Sexual dimorphisims, or sex limited characters are present from very low types of plants and animals and continue to the highest representatives of both kingdoms. The general nature of sex-limited characters differs in no wise in the higher forms from the lower except that the higher may have a much greater complexity of hereditary factors that may be influenced by the sexual state in their expression.

The presence of allosomes in a few plants and in apparently all of the higher animals complicates the study of sexuality and must be carefully considered, as well as the mode of transmission of the hereditary potentialities, if proper deductions are to be made as to the nature of sexuality in such forms. Heteromorphic allosome mates plainly have differences in hereditary factors and since these chromosomes have a peculiar and usually definite distribution in relation to the sex of the individual, they give rise to characteristic sex-limited sex-influenced, and sex-associated characters.

It is the intention to present in a very brief way an explanation of certain phenomena from the standpoint of the functional nature of sex in order to make clear to students who deal

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mainly with plant materials that there is nothing in the animal series that is incompatible with a consistent theory of sexuality as it is developed in plants and in lower animals. The writer has found that much confusion of mind does exist, obtained mainly from impossible hypothetical explanations of certain common types of animal heredity. These hypotheses have been highly elaborated and may appear quite plausible to one unacquainted with a great array of facts and phenomena of sexuality met with not only in plants but also in the lower animals, which flatly contradict the hypotheses and which their advocates have never attempted to consider.

Since heredity is a manifestation of the protoplast, a cytological interpretation must be developed as the basis of all speculations which go beyond observation. But since the hereditery character is the result of an expression through physiological activity, it follows that the dead cell inclusions and the physical state of the protoplasm itself at the time of expression may have a decided effect on the character developed. Now since sexuality is a condition or state of the individual, organ, cell, or chromosome, which may come and go and which can be reversed, it follows that the sexual characteristics of an individual may not always correspond to the actual allosome constitution, present. But whether allosomes are present or not, tissues or individuals genetically the same may show entirely different sexual characters in different parts of the body, depending on which sexual state is present during the development of the part. Such characters distinctive of male or female individuals or of parts of hermaphroditic individuals are sex-limited characters. The first step in developing an adequate conception of sex-limited characters is to study the dimorphisms in hermaphrodites and bisporangiate individuals and then proceed from the basis established to the dimorphisms of unisexual and monosporangiate individuals. Sex-limitation in monecious sporophytes may consist in the presence of a character or its complete or nearly complete suppression through one sexual state or the other, as for example the awn on the lemma of *Zizania aquatica* which is present on the carpellate spikelet but undeveloped on the staminate spikelet. In other cases there is merely a degree of difference of development or expression, as in *Cocos nucifera* in which the sepals of the staminate flowers are small and those of the carpellate flowers much larger; or as in the inflorescence of *Sicyos angulatus*

where the staminate inflorescence has a long peduncle and the carpellate inflorescence a short one. There are exactly similar differences in cases of unisexual and monosporangiate individuals. For example in Dorset sheep, the female has little horns and the male large ones, while in the Merino the males have horns and females have none. In *Carica papaya*, a diecious plant, the staminate corollas are sympetalous and the carpellate corollas are choripetalous. In the diecious *Acnida tamariscina*, the staminate flowers have a five-sepaled calyx, while the carpellate flowers have none.

Characters that are sex-limited may have their factors or potentialities either in the autosomes or in the allosomes. Recently it has become the vogue, in some quarters to rechristen the allosomes as "sex-chromosomes" and the characters, whether sex-limited or not, which have their potentialities in the allosomes as "sex-linked" characters. Now all chromosomes of sexual organisms are sexual chromosomes. There are no special factors or determiners for sex, nor sex-linked factors properly speaking. There is no "sex-linked heredity". Such terminology can only arise out of ignorance of sexuality as it is evolved in the organic kingdom and leads only to confusion and misunderstanding of things as they actually exist. Both terms are wrong because they tend to perpetuate an inadequate hypothesis of sexuality as well as a false notion as to the distribution of sexual characters. For example, when we say that ordinary Daltonism is "sex-linked" the term might naturally imply that the color-blindness was confined to one sex. But women are color-blind as well as men. Futhermore, when there is sex reversal, whether affecting the primary or secondary sexual state, the so-called "sex-chromosomes" do not at all indicate the sex of the cell or individual. The terms are improper also from the point of veiw of sexuality itself, since they imply that sex is a matter of Mendelian or chromosome heredity. The common occurrence of sex-reversal in both directions and the fact that commonly in plants the sex is not determined nor changed when the chromosomes, with their Mendelian heredity, are segregated show that fundamentally sex is primarily a thing apart from Mendelian heredity. Nor is sex usually determined in plants when chromosomes are aggregated in fertilization. In all vascular plants except the comparatively rare unisexual gametophytes of the homosporous pteridophytes and the diecious sporophytes of seed plants, both male and

female conditions arise from the same chromosome complex in the same individual, and futhermore, as stated, the sex can frequently be reversed in either direction in both haploid gametophytes and diploid sporophytes.

Sphaerocarpus seems to be the only known case in both the plant and animal kingdoms, where allosomes presumably might control or determine directly the primary sexual state and structures in a haploid organism, and here these states follow the presence of the secondary sexual states in the gametophytes. In animals as in the plants where such bodies are present, the segregated allosomes seem to have no influence whatever on the development of the primary sexual states or on the development of the primary sexual structures of the gametes. Then what is the basis for the assumption of a fundamental influence in the zygote?

From a correct, evolutionary point of view it is evident that the allosome condition is the result of sexuality rather than its cause. It is only in the most extreme type of sex-determination in the gametophyte, where the sex is determined in the spore, that a differential distribution of chromosomes could arise, which could influence functional states; and in the final development of dieciousness, there is again a condition established in which allosomes with differential heredities could be evolved and continued in a definite sex-association in the individual.

At most, allosomes might be the cause of the diecious conditions or of some unisexual individuals whether diploid or haploid; but this is only one of the special aspects of sexuality, not the important problem to be solved, either of primary sexual states and characters, or of secondary states and characters. It must be remembered that sexual dimorphism is just as wide-spread and prominent in the individual in species without evident allosomes, like the hemp for example as in species with allosomes (See Schaffner 19, 22, and McPhee 10.) But allosomes are not at all an explanation of unisexuality; for all of the 150,000 species of heterosporous plants have unisexual gametophytes, and in not a single one of these has the unisexual condition any relation to allosomes. The very nature of the life cycle makes such a relation impossible.

So far as we have present knowledge, we can have chromosome-linked heredity or factors and perhaps cytoplasm-linked and plastid-linked heredity. Chromosome heredity falls into

two categories, autosome-linked heredity and allosome-linked heredity, but the hereditary factors or potentialities of autosomes and allosomes are essentially the same in nature, since organisms with allosomes show nothing fundamentally different from those which have no such bodies.

Sex-limited characters are physiological as well as morphological. The instinctive characters peculiar to one sex or the other are readily reversible, as has been known for a long time, as well as the morphological characters. Now if our notions of Mendelian heredity are correct, all sex characters which are of a unitary nature must in the end be due to one or more hereditary factors. These factors, as understood at present, are presumably chromosome-linked; that is, they are properties of certain chromosomes or parts of chromosomes. For convenience we can assume that they are in the chromatin granules as Mottier (15) suggested in 1907.

As intimated before, the autosome-linked factors give rise to one type of sex-limited characters and the expression is the same whether it occurs in either hermaphroditic or bisporangiate individuals on the one hand, or in unisexual or monosporangiate individuals on the other. Whenever a given sexual state is present, the factors in the autosomes express a peculiar character or group of characters that we recognize as male or female as the case may be. The expression changes with the change of sexual state. This is evident both in monecious plants and in reversed diecious individuals.

Since the allosomes show a peculiar distribution in relation to the sex of the individual any factors they may have may show a peculiar association with one sex or the other, while characters which have their potentialities in the autosomes will show no special associative peculiarities in relation to either sex when Medelian segregation occurs. Any factors in the allosomes subject to sex-limitation can, of course, only show the characters where they are actually present in the proper sexual state. Such characters are sex-limited characters of allosome-linked herdity. Allosomes may have herdity not sex-limited the same as have the autosomes. Such heredity will show a peculiar distribution in relation to sex in reciprocal crosses.

The writer does not wish to discuss in all its details the probable cause for the definite distribution of allosomes in relation to male and female sex, but it can be definitely stated that this condition, whether ascribed to specific, differential

attraction or whether we assume that the allosomes are sex-producing through their influence on the functional activity of the cell, is not at all antagonistic to the physiological theory of sex. Because of the ease with which certain allosome-bearing plants and animals change their sexual states under certain conditions, the writer inclines strongly to the differential compatibility hypothesis at the present time. The assumption of a greater or less degree of specfic compatibility or incompatibility and of a consequent specific attraction and selective union of gametes with allosome differences together with a changing metabolic gradient modifying the primary sexual state of the eggs of heterogamous organisms brings the situation as presented by the allosome-bearing organisms into complete harmony with that found in hermaphrodites and bisporangiate sporophytes of the various types as well as with that found in those strongly dimorphic unisexual and diecious species, in which no allosomes are present. The nature of sex-determination in relation to allosome will be further discussed below in connection with the special problems of allosome heredity and sex-limited characters.

Since X and 2X are established symbols in an extensive botanical literature and are still almost universally used by botanists to designate the haploid and diploid complements of chromosomes, X and Y cannot properly be employed as symbols for allosomes without causing an endless amount of confusion in both morphology and genetics. In the present paper A and B will be used as symbols instead of the much used but confusing symbols "X" and "Y" and "W" and "Z". "A" represent the allosome which in diploid individuals is normally associated with either sex; "B" represents the allosome which in diploid individuals is normally associated with but one sex. Whenever we have the allosome formulæ ♀ AA and AB♂, or ♀ AB and AA ♂, or ♀ Ao and AA ♂ there is apparently indiscriminate migration of the A allosome to either sex, just as in the case of autosomes, but the B allosome under the normal conditions is associated with a single sex, either the male only or the female only.

Although there are many peculiar types of allosome constitution, the most common types of animals and plants in relation to the allosome condition are the seven presented below. A and B represent the allosomes, and X the haploid complement of autosomes or the chromosomes in general when no allosomes are present.

I. MAN, DROSOPHILA, etc. (See Painter (20) and Stevens (29).

♀ $\frac{AA}{xx}$, $\frac{AB}{xx}$ ♂. Diploid individuals.

Eggs = $\frac{A|}{x}$, $\frac{|A}{x}$. Determined as ♀ $\frac{A|}{x}$ and $\frac{|A}{x}$ ♂.

Sperms = $\frac{A|}{x}$, $\frac{|B}{x}$.

In some mammals decided reversals of secondary sexual characters have been observed.

II. ABRAXAS. (Probably). No cytological difference visible. (See Doncaster (4).

♀ $\frac{AB}{xx}$, $\frac{AA}{xx}$ ♂. Diploid individuals.

Eggs = $\frac{A|}{x}$, $\frac{|B}{x}$. Determined as ♂ $\frac{A|}{x}$ and $\frac{|B}{x}$ ♀.

Sperms = $\frac{A|}{x}$, $\frac{|A}{x}$.

In this allosome type remarkable sex-intergrades have been developed by crossing species. (See Goldschmidt (7).

III. CHICKEN. (See Guyer (9).

♀ $\frac{Ao}{xx}$, $\frac{AA}{xx}$ ♂. Diploid individuals. o = zero.

Eggs = $\frac{A|}{x}$, $\frac{|o}{x}$. Determined as ♂ $\frac{A|}{x}$ and $\frac{|o}{x}$ ♀.

Sperms = $\frac{A|}{x}$, $\frac{|A}{x}$.

Decided sex reversals observed; female individuals reversed to secondary male state and even to the normally functioning primary male state; males, so far, reversed to secondary female state only.

IV. SPHAEROCARPUS. (Plant). (See Allen (1).

Sporophyte = $\frac{AB}{xx}$ Neutral. Diploid individuals.

Spores = $\frac{A|}{x}$, $\frac{|B}{x}$. Determined as ♀ $\frac{A|}{x}$ and $\frac{|B}{x}$ ♂.

Gametophytes = ♀ $\frac{A|}{x}$, $\frac{|B}{x}$ ♂. Haploid individuals.

Gametes = ♀ $\frac{A|}{x}$, $\frac{|B}{x}$ ♂.

No sex reversal known.

V. EQUISETUM ARVENSE and OSTRICH-FERN. (See Wuist (32). No allosomes present.

Sporophyte = $\frac{oo}{xx}$ Neutral Diploid individuals.

Zero (o) = absence of allosome.

Spores = $\frac{o|}{x}$, $\frac{|o}{x}$. Determined as ♀ $\frac{o|}{x}$ and $\frac{|o}{x}$ ♂.

Gametophytes = ♀ $\frac{o|}{x}$, $\frac{|o}{x}$ ♂. Haploid individuals.

Gametes = ♀ $\frac{o|}{x}$, $\frac{|o}{x}$ ♂.

Complete primary and secondary sex reversal easily brought about; female to male and male to female. The male to female reversal much less frequent than the reciprocal reversal.

VI. CANNABIS SATIVA. (See McPhee (14). No allosomes present.

Sporophyte = ♁ $\frac{00}{XX}$, $\frac{00}{XX}$ ♀♂. Diploid individuals strongly sexually dimorphic.

Spores = ♀ $\frac{0}{X}|$, $|\frac{0}{X}$ ♀. Megaspores with secondary sexual dimorphism

and ♂ $\frac{0}{X}|$, $|\frac{0}{X}$ ♂. Microsphores with secondary sexual dimorphism.

Gametophytes = ♀ $\frac{0}{X}|$, $|\frac{0}{X}$ ♀ and ♂ $\frac{0}{X}|$, $|\frac{0}{X}$ ♂. Haploid individuals very strongly sexually dimorphic.

Gametes = ♀ $\frac{0}{X}|$, $|\frac{0}{X}$ ♂. Primary sexual state.

Female gametes before or after fertilization = ♀ $\frac{0}{X}|$, $|\frac{0}{X}$ ♂.

Both partial and complete sex-reversal easily brought about, carpellate to staminate and staminate to carpellate.

VII. HUMULUS JAPONICUS. (See Winge (31).

Sporophytes = ♁ $\frac{AA}{XX}$, $\frac{AB}{XX}$ ♀♂. Diploid individuals slightly sexually dimorphic, decidedly so as to the inflorescence.

Spores = ♀ $\frac{A}{X}|$, $|\frac{A}{X}$ ♀ and ♂ $\frac{A}{X}|$, $|\frac{B}{X}$ ♂.

Gametophytes = ♀ $\frac{A}{X}|$, $|\frac{A}{X}$ ♀ and ♂ $\frac{A}{X}|$, $|\frac{B}{X}$ ♂. Supposed allosomes have no influence on the sex of the gametophyte.

Gametes = ♀ $\frac{A}{X}|$, $|\frac{A}{X}$ ♀ and ♂ $\frac{A}{X}|$, $|\frac{B}{X}$ ♂. Primary sexual state.

Female gametes before or after fertilization are ♀ $\frac{A}{X}|$, $|\frac{A}{X}$ ♂.

Both partial and complete sex-reversal easily brought about, carpellate to staminate and staminate to carpellate.

On the basis of the cytological conditions and of the physiological theory of the nature of sex, the various possibilities of transmission and expression of the more common types of heredity in relation to sex are considered below. This is not to be regarded as an exhaustive analyis, however.

In relation to allosome-linked heredity and sex limitation we can have the following specfic conditions:

1. Only the females are affected both by a single dose and by a double dose. Various types of hologynic heredity.
2. Only the males are ever affected both by a single dose and by a double dose. The various types of holoandric heredity.

3. Only the females (unpaired allosome condition) are ever affected, the heredity needed for the effect coming from the male. Dia-andric heredity.
4. Only the males (unpaired allosome condition) are ever affected, the heredity needed for the effect coming from the female. Diagynic heredity.
5. Both males and females are affected by a single dose, the heredity coming from either parent as a carrier. Ordinary dominant heredity and criss-cross heredity of the allosome condition in the chicken.
6. The females (homomorphic allosomes) affected only by a double dose, the males (heteromorphic allosomes) affected by a single dose. Daltonism, etc.
7. The males (homomorphic allosomes affected only by a double dose, the females (heteromorphic allosomes) affected by a single dose. The opposite of Daltonism. It should be possible in the Abraxas and chicken types of allosome constitution.
8. The females (heteromorphic allosomes) not affected, the males (homomorphic allosomes) affected by a double dose only. One type of holoandric heredity.
9. The males (heteromophic allosomes) not affected, the females (homomorphic allosomes) affected by a double dose only. One type of hologynic heredity.

Since sex is developed in the cell or in the individual in various degrees of intensity and persistency, a low condition of maleness or femaleness may not inhibit or only partially inhibit in specific instances a given heredity so that exceptions to the statements may appear.

Now considering the various possibilities under each of the seven types of chromosome constitutions tabulated above, a definite program can be laid out by which any given case of herditary transmission and its sex-limitations can be studied and defined.

I. Human and Drosophila Type.

The type of chromosome constitution in which the female is homomorphic and the male heteromorphic for the allosomes "A" and "B", well established by cytological evidence (Painter 20, Stevens 29), may give rise to the following conditions, if A has a sex-influenced factor "*k*" and B has a sex-influenced factor "*l*."

1. A may have a factor *k* latent in the cell in the presence of the male state and in the presence of B.
2. A may have a factor *k* active in the cell in the presence of the male state and in the presence of B.

3. B may have a factor *l* latent in the cell in the presence of the male state and in the presence of A. The factor could only appear in case of sex reversal or abnormal allosome or chromosome associations.
4. B may have a factor *l* active in the cell in the presence of the male state and in the presence of A.
5. A may have a factor *k* latent in a single dose in the presence of the female state when associated with an allosome A without the factor.
6. A may have a factor *k* which is active even in a single dose in the presence of the female state when associated with an allosome A without the factor; and of course then also active in double dose.
7. A may have a factor *k* which is active only in a double dose in the presence of the female state.
8. A may have a factor *k* which is latent even in double dose in the presence of the female state.

Abnormal cases are produced by ordinary sex-reversal or by abnormal sex-determination because of the presence of supernumerary autosomes or allosomes in the cell, among which are the following:

9. B may have a factor 1 which may become active in the presence of a female state, although it shows no activity when the cell is in the normal male condition.
10. A alone, with a factor *k* might show activity of the factor when B is absent and in the presence of the male state.
11. A alone might have a factor *k* that is latent because of the absence of B and in the presence of the male state.

Ordinary Daltonism or red-green color blindness in man is apparently an example of cases "2","5", and "7". Records have been established of 7 color blind women who had between them 17 sons, all color blind.

A certain type of senile cataract as reported by Enriques (6) is apparently an example of cases "1", and "6".

Schofield's (27) pedigree of webbed toes in man is apparently an example of case "4," or of "2" and "8".

The terms diagynic, dia-andric, hologynic, and holoandric heredity as used by Enriques (6) would be convenient but they are apparently too limited in their scope for general use to cover all the different types of hereitary transmission and expression and will need to be extended, either by modifying phrases or otherwise, when all the modes of allosome-linked and autosome-linked heredity and the relation of the factors to sex-limitation are known.

In the human type of allosome constitution, namely ♀ AA, AB ♂ :

1. If B has a factor *l*, active in the presence of the male state, it can only be transmitted from male to male. If B has a factor *l*, latent in the male state, it will be transmitted directly from male to male but will never show except possibly in case of sex-reversal.
2. If A has a factor *k* which is active only in double doses in the presence of femaleness and not active in the presence of the male state, then none of the offspring of an affected female will have the character unless the unaffected male parent is a carrier in which case all the daughters will be affected and the sons will, of course, be carriers.
3. If A has a factor *k* active in the presence of the male state it can not be transmitted to the sons directly but only from a mother.
4. If A has a factor *k* active in the presence of the male state but only active in double dose in the presence of the female state then it can only be transmitted directly to the male from an affected or unaffected female, in the latter case only half the sons showing the character; but to produce an affected daughter the father must be affected and the mother either affected or a carrier, in the latter case half the daughters being affected. In specific instances affected male offspring may be appearing from the line and possibly affected females for a long time, until a female carring the factor is mated with an affected male.
5. If A has a factor *k* latent in the presence of the male state and B, but active in single dose in the presence of the female state associated with another A without the factor, and active also in double dose, then the character must be confined entirely to the female line and will appear in all the daughters if the mother has a double dose or if the father alone is a carrier. If the mother alone has the character and the heredity in single dose, half the daughters will be affected and half the sons will be carriers.
6. If A has a factor *k* which is latent even in double dose in the presence of the female state but active in the presence of the male condition, then the character will be confined to the male line but is transmitted to the sons only through the unaffected mother.

Any hypothesis as to which allosome has the heredity potentiality in any specific case can be tested out to a certain extent by breeding experiments, especially if sex reversal occurs sporadically or can be produced experimentally.

In man and Drosophila, etc. the allosomes are homomorphic in the female and heteromorphic in the male according to the scheme of A and B as outlined above. But in certain animals like Abraxas apparently, the male has the homomorphic set and the female the heteromorphic. According to Guyer's (8 and 9) cytological studies, the male somatic cells of the common chicken show two allosomes while the female somatic cells show only one of these bodies. In this case then, as indicated the allosomes are all of the type A and the female

contains an unpaired A. In spermatogensis the two allosomes seem to pair and pass undivided to one pole, which would thus result in two spermatozoa each with an allosome and two without allosomes. The eggs presumably are formed half with an allosome and half without. Now to obtain the proper somatic condition, three possible things may happen: 1st., the spermatozoa without allosomes may not develop properly or, if they develop, fail to develop the primary sexual state completely; 2nd., the sperms may all develop properly but the eggs lacking the allosome may fail of normal development; or 3rd., all the eggs and sperms may develop properly but there is a lack of specific compatibility or an indifference between the eggs and spermatozoa without allosomes, or if these can conjugate the resulting zygote may be unable to develop. It is supposed, because of the results of the measurements of the spermatozoa, that the first assumption is the most probable.

We can assume that in the higher plants and the higher animals also, if the sexual state is determined in the gametes it is always determined in the egg, namely the sex which is continued in the developing individual; for apparently the sperm is too extremely differentiated into a male cell to pass over into the female state without passing through a semingly impossible de-differentiation. Only in the very lowest sexual plants, like Spirogyra, for example, is it possible that a male gamete can pass over into the female state and this is actually known to occur occasionally. On the other hand it is well known that in the higher plants even a sister cell of the egg may pass to the minus or male state and conjugate with it. Occasionally sperms of some of the higher green algae have evolved to the condition in which they may pass back to a vegetative development as in certain species of Oedogonium, but in such cases a dwarf male is always the result.

When the eggs are homomorphic and the sperms heteromorphic, with AA ♀ and AB ♂ allosome sets, as in man, we can make three hypotheses as to sex-determination:

1. The haploid eggs having the same heredity and the same chromosome complement, the sex is determined by some physiological balance the same as in all cases of sex-determination in heterosporous, bisporangiate, diploid sporophytes; in haploid, hermaphroditic gametophytes in diploid hermaphroditic gametophytes; and in diploid, hermaphroditic animals; as well as in all cases of sex-reversal in diploid, monosporangiate sporophytes; in haploid, unisexual gametophytes; or in diploid unisexual animals or plants, whether allosomes are present in their cells or not.

Following this determination of the physiological gradient in the direction of one sexual state or the other there is a differential specific attraction with the more compatible kind of sperm, the egg determined toward maleness attracting the sperm with the allosome B, with its peculiar hereditary constitution, and the egg determined toward femaleness attracting the sperm with the allosome A. In this case the sex would actually be determined while fertilization is taking place, but it may also be normally completely determined before coming in contact with the sperm, but this does not mean that the sexual state is completely developed any more than that a new born child has its cells in a completely sexual, male or female state.

Not only do we know of the compatibility and incompatibility of the gametes of the same and of dissimilar species but in the synapsis of the chromosomes there is evident a very decided compatibility of synaptic mates and apparently a very decided incompatibility of chromosomes which are not mates. Moreover the differential parasitic growths of pollentubes is well known, which results in decidedly disturbed Mendelian ratios.

2. All the eggs may be in the same physiological condition at the time of fertilization, and attraction and union may take place purely by the law of chance and after fertilization the presence of the given type of allosome will produce a metabolic level that will throw the fertilized egg invariably toward the one sex, that with the allosomes AA toward femaleness and that with the allosomes AB toward maleness. There is nothing incompatible in this hypothesis with the physiological theory of sex. The sex is determined in exactly the same way as when determined or reversed in the vegetative tissues of the body, the special allosome merely giving the proper physiological state under the normal conditions. The allosomes are *merely sex-producing* having a direct effect on the physiology of the protoplast. The main difficulty with the hypothesis is that if the allosomes are thus sex-producing, the sexual state should remain unchanged so long as the bodies are present, which is plainly not the case in the great number of examples in which both secondary and primary sexual states are reversed in the individual. As stated, we have no objection to any one holding this second hypothesis provided he can give a convincing explanation as to why allosomes are specific and invariable sex-producers immediately after fertilization, before any specific sex is established, but cannot hold the sex after the soma is developed and a given sexual state thoroughly established.

3. There is not only random mating but the allosomes are Mendelian sex determiners in the same way as the autosomes determine the ordinary Mendelian characters, the female being homozygous and the male heterozygous for sex or vice versa. The allosomes are real "sex chromosomes". This third hypothesis is, however, so contradictory to the mass of known facts in relation to sexuality, so monstrous a misfit as an explanation of maleness and femaleness as it appeared and evolved in both the plant and animal kingdoms, that the wonder is that it could ever have been taken seriously as a scientific explanation of the facts of sexuality that have so far been amassed.

When the eggs have similar allosomes, therefore, the sex, either male or female, is determined by a physiological balance the same as in organisms without allosomes as for example in monecious species and in various diecious plants like the hemp where allosomes are apparently lacking. Now this balance may be conceived of as a certain point in the metabolic gradient of the cell or tissue involved. If the metabolism falls to one side the condition leads on to femaleness, if to the other to maleness for the given species. In some diecious plants, as in Arisaema triphyllum, the sexual state may not be developed in the egg at all but at a later stage and the physiological balance appears to be such that probably the sex is at first always thrown to maleness, although this is not yet entirely certain. The writer found a strong tendency toward maleness in young offshoots, no difference whether the parent corm was for the time being producing staminate or carpellate shoots.

In cases where the eggs have the heteromorphic allosomes, or where part of the eggs have an allosome and part have none we may consider that the sexual states arise in the same fundamental way as in other cases, but that the egg without the allosome or with the B type of allosome is thrown to femaleness while the A-containing egg is thrown to maleness. In this case no selective mating could arise and no incompatibility in relation to allosomes, unless the given egg under certain conditions, produced no reaction whatever in the sperms in which case individuals of only one sex would be produced at the time, for under the allosome conditions considered the sperms would all be alike. If any one objects with the proposition that the egg with the allosome should be thrown to femaleness and the one without to maleness, then we can only direct them to the condition in the flowers of the Anthophyta where the determinate floral axis always passes to the male state first and then to the female state near the end of the determinate growth; and also to a certain type of monecious inflorescence, the axis of which always develops the female state first with carpellate flowers and later the male state with staminate flowers, toward the end of the determinate growth when theoretically we might expect the opposite to take place. But as intimated above, in chickens the sperms without allosomes may develop and the eggs without allosomes may fail to function, in which case all the eggs would have the same type of allosome and a balance could be established through a physiological gradient.

In birds and similar cases therefore, the sex is determined in the egg apparently according to the allosome constitution, the allosome determining the physiological state. The egg without the allosome is determined as female that with the allosome as male. This is contrary to the usual assumption that the greater quantity of chromatin determines femaleness. But on the physiological basis of sex determination, the allosome associated with the male condition either single, as in the unfertilized egg, or double, as in the individual, may have factors which depress the nutrient level, so the absence of the allosome with the absence of these physiological factors would tend to produce femaleness. After fertilization the male has two of the A. allosomes and the female one A. It is, therefore, only a matter of degree or intensity of influence and we would then expect that the female could be changed to a male or the male to a female condition without great difficulty as is actually done by experiment at the present time.

Although the quantitative theory of sex, as developed by Goldschmidt, comes much nearer to the facts of sex determination and expression than the homozygous-heterozygous Mendelian hypothesis, which has up to the present been so blindly and enthusiastically accepted; it will be evident to any one familiar with the fact of experimentally induced sex reversals and re-reversals in unisexual individuals, as accomplished by the writer, as well as from a host of other phenomena, that any balance of genes imagined cannot be an explanation of sex determination and sexual dimorphism, since the change from one sex condition to the other and then back again is brought about during vegetative growth by ecological means, without disturbing, by aggregation or segregation, any balance of genes that might be present.

II. Abraxas Type.

The allosome formula is apparently ♀ AB, AA ♂. In general the conditions of activity and latency in relation to sex will be just the opposite from those in the human type.

1. A may have a factor *k* latent in the cells in the presence of the female state and in the presence of B.
2. A may have a factor *k* active in the presence of the female state and in the presence of B.

3. B may have a factor *l* latent in the cell in the presence of the female state and in the presence of A. This could never appear in character except in cases of sex reversal.
4. B may have a factor *l* active in the cell in the presence of the female state and in the presence of A.
5. A may have a factor *k* latent in a single dose in the presence of the male state when associated with an allosome A without the factor.
6. A may have a factor *k* which is active even in single dose in the presence of the male state when associated with an allosome A without the factor, and of course then also active in double dose.
7. A may have a factor *k* which is active only in a double dose in the presence of the male state.
8. A may have a factor *k* which is latent even in double dose in the presence of the male state.

Irregularities in allosome and chromosome distributions and sex reversals may, of course, occur as in the ♀ AA, AB ♂ type and produce unusual results in relation to sex limitation.

In Abraxas the grossulariata color as contrasted with the lacticolor is evidently a case of "2" and "6". The characters are not at all sex-limited or "sex-linked" but appear in either sex according to the ordinary Mendelian expectation limited, however, by the particular mode of migration of the allosomes. They are characters expressed by allosome-linked factors.

In the Abraxas type the heredity in relation to the allosomes may be transmitted as follows:

1. If B has a factor *l* active in the presence of the female state, it can only be transmitted from female to female. If B has a factor *l* latent in the female state, it could never show normally except in case of sex reversal.
2. If A has a factor *k* which is active only in double dose in the presence of maleness and not active in the presence of the female state then none of the offspring of an affected male will have the character unless the unaffected female parent has the factor also in which case the male offspring will be affected and the female offspring will become carriers.
3. If A has a factor *k* active in the presence of the female state and in the presence of B it cannot be transmitted to the daughters directly but only from a father.
4. If A has a factor *k* active in the presence of the female state but only active in double dose in the presence of maleness then it can only be transmitted directly to the female from an affected or unaffected male.
5. If A has a factor *k* latent in the presence of the female state and of B but active in single dose in the presence of the male state and another A without the factor and active also in double dose in the presence of the male state, the character will be confined entirely to the male line.

6. If A has a factor *k* which is latent even in double dose in the presence of the male state but active in the presence of the female state then the character will be confined to the female line but is transmitted to the female offspring only through the unaffected male parents.

III. Chicken Type.

The allosome formula is apparently ♀ Ao, AA ♂, the cells of the normal female having a single allosome.

1. A may have a factor *k* latent in the cell in single dose in the presence of the male state.
2. A may have a factor *k* active in the cell in single dose in the presence of the male state and, of course, also in double dose.
3. A may have a factor *k* active only in double dose in the presence of the male state.
4. A may have a factor *k* latent even in double dose in the presence of the male state.
5. A may have a factor *k* latent in single dose in the presence of the female state.
6. A may have a factor *k* active in single dose in the presence of the female state.

When sex-reversal takes place, which is comparatively frequent in the case of the hen, latent factors in the allosome as well as sex-limited factors in the autosomes may become active. Chickens apparently furnish favorable material for the study of allosome-linked and sex-limited heredity.

Any factor in A active in the female state can be derived only from the male parent directly, so until the normal heredity is established in a cross, great care must be taken else a desirable factor may be lost. Taking into account the allosome formula, the migration of the allosomes and the condition of any factors which the allosomes contain the hereditary transmission can easily be worked out.

Taking the well-known case of the golden Sebright and silver Sebright bantam chickens and assuming again that the eggs are heteromorphic and the sperms homomorphic in respect to allosomes because of the failure of the allosome-lacking spermatids to develop properly, then we can explain the breeding results (see Punnett 21) as follows:

Suppose that "silver" is dominant and "golden" recessive and that these factors are in the allosomes A, and suppose that the eggs with allosome A are determined as males and the eggs without allosome A are determined as females. Then crossing

golden Sebright ♀ with silver Sebright ♂ will give only silver females and only silver males; for both types of eggs will get an allosome A containing the factor S.

Silver Sebright ♀ crossed with golden Sebright ♂ will give golden females and silver males, because the females will get an allosome with factor g (golden) and have no silver while the males would have an allosome with golden and also one with the dominant silver.

The F2 from the F1 of the first cross will give both silver and golden females but only silver males; for the eggs will be half without and half with the A allosome containing the factor for silver and the sperms will be half with allosome A containing the factor for golden and half with allosome A containing the factor for silver which will thus always give a male with at least one dose of silver.

The F2 from the F1 of the second cross will give both silver and golden females and both silver and golden males; for the eggs will be without the allosome or else have the allosome A containing the factor for golden and the sperms will have either the allosome A with the factor for golden or the allosome A with the factor for the dominant silver. So the allosome-lacking egg can receive either allosome A (g) or allosome A (s) and the other type of egg will have only the allosome A (g) which on conjugating with one or the other type of sperms will produce a zygote homozygous for golden and the other heterozygous for the dominant silver.

The characters are, therefore, not at all sex-limited nor "sex-linked" but are in plain language non-sex-limited characters whose factors are allosome-linked.

The familar example of the cross between non-barred Cornish Indian Game chickens and Barred Plymouth Rocks is of the same nature as well as various other sets of allelomorphic characters whose potentialities presumably are in the allosome A.

IV. Sphaerocarpus Type.

Since the sporophyte is homosporous no sexual dimorphism is possible in it but hereditary factors in allosome A or in allosome B may be active and if this is the case characteristic hereditary transmissions would appear. The gametophytes having the haploid complement of chromosomes and each kind of allosome being constantly associated with one sex, any

allosome-linked factors could only produce characters in the one sex unless sex-reversal takes place. Any sex-limited character or any character not sex-limited whose factors are in the allosomes would show a 1 to 1 ratio. Any factor in allosome A would give a character constantly associated with femaleness and any factor in allosome B would give a character constantly associated with maleness. In case of a heterozygous condition of a sex-limited factor in the autosome any gametophytic character will appear in half the males or in half the females as the case may be.

V. Equisetum arvense Type.

The sporophyte is homosporous and can normally have no sexual dimorphism. There are no allosomes but the haploid gametophytes are determined in the spores or in the early stages of germination as female and male individuals with ordinary sex-limited characters. Both gametophytes can be reversed and the newly developed parts will then show the opposite sex-limitation. Factors which are heterozygous in the sporophyte will show equal segregation and will show equal ratios in the two sexes; while any such heterozygous factors that give rise to sex-limited characters in the gametophytes will also show in half the individuals of the sex involved.

VI. Cannabis sativa Type.

No allosomes being present in the diecious hemp, the sex is determined in the eggs of like hereditary constitution either before or after fertilization and the potentialities of the sex-limited sporophytic characters, which are numberous, are all in ordinary chromosomes. In case of sex-reversal all the sex-limited characters of the opposite sex that can be developed in the reversed parts appear. No heredity or condition of any kind is known to influence the sex of the gametophytes although the sporocytes may undergo sex-reversal. The haploid complement of chromosomes will show male sex-limited characters in the pollen grains no difference what the hereditary complex may be, after male determination in the sporophyte; and the same complement of chromosomes will show female sex-limited characters in the female gametophytes after female determination in the sporophyte. The sex is not affected by the reduction division. Whether any specfic factors give rise

to sex-limited characters in both gametophyte and sporophyte is not known. Since sex-reversal is easily accomplished, characters latent and normally never appearing in the sex present will show in the reversed branches and thus reveal the presence of heredity in the given individual which could otherwise only be inferred.

VII. Humulus Type.

Any allosome-linked herdity and sex-limitation in general will be expressed in the same way in the sporophyte as in Man and Drosophila. The sex of the gametophytes has no relation to the allosome distribution but follows that which was present in the flowers which produced the spores from which the gametophytes originate. Abundant sex reversal is produced in the sporophyte, the male to the female and the female to the male, by means of a short daily illumination period. The carpellate plant with the homomorphic set of allosomes possesses all the factors or potentialities of both sexes the same as the staminate plant with the heteromorphic set of allosomes. The homozyous-heterozygous sex formula is thus a figment of the imagination.

The Five General Types of Hereditary Expression.

The five general types of hereditary expression as influenced either by primary or secondary sexual states may then be summarized as follows:

1. The peculiarity of inheritance produced by dominance and recessiveness through which an individual shows characters transmitted directly from one parent only, which characters have no relation to the special sex of the individual or any part of the individual under the influence of a sexual state, their factors being influenced only by the ordinary physiological conditions or gradients which cause them to be active or latent for the time being. These are the ordinary Mendelian heredities often observed to be handed down from father to daughter or from mother to son, or vice versa in either case. The factors are autosome-linked or, in case there are no allosomes, merely chromosome-linked, and the characters are not sex-limited.

2. Sex-limited or sex-influenced heredity, the factors being autosome-linked and expressing characters either through direct influence or through latency or activity brought about by the presence of one sexual state or the other. These are the ordinary sex-limited characters producing sexual dimorphism either between entire individuals or different parts or cells of the same individual.

3. Hereditary characters whose factors are in the allosomes, on account of which they receive a distinctive distribution in transmission not sex-limited or sex-influenced in nature however.

4. Hereditary characters which have their factors in the allosomes and are sex-limited in single dose through the action of one sexual state or the other.

5. Hereditary characters which have their factors in the allosomes and which are sex-limited in double dose through the influence of one sexual state or the other.

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